

RESEARCH PAPER

Assessment of salt tolerance in Algerian oasis wheat landraces: An examination of biochemical, physiological, and agronomical traits

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Abstract

Wheat landraces cultivated in the oases of Algeria are known for their resistance to abiotic stresses as a result of the extreme environmental constraints of the Sahara. As such, these landraces represent valuable breeding material for improving abiotic stress tolerance in wheat. This study was conducted to evaluate salt tolerance of bread and durum wheat from the Algerian oases. Ten wheat landraces from the Algerian oases were grown under prolonged salinity stress (150 mM NaCl) in greenhouse conditions. Data were assessed for 19 physiological, biochemical, and agronomical traits. The wheat landraces exhibited considerable variation in their salinity stress tolerance. The membership function value of salt tolerance identified Oum RokbaElhamra, Khellouf and Zeghlou as the most tolerant landraces while Bourione was identified as sensitive. The salt-tolerant and moderately tolerant wheat landraces maintained stable yields under conditions of salinity stress. Regression models constructed from MFVS and salt tolerance coefficients showed that for bread wheat, amino acid content and grain yield accounted for most of the variation in MFVS, while for durum wheat, the number of grains per plant and Na⁺ content explained the majority of observed differences in MFVS. Correlation analysis showed that the MFVS was significantly associated with grain yield, selectivity between K⁺ and Na⁺, and plant height. The results confirm that Algerian oasis wheat landraces are a valuable source given their salt tolerance and could be utilized in breeding programs seeking to improve salinity stress resilience in wheat.

Keywords

Grain yield, membership function value, Sahara, salinity, abiotic stress

Introduction

Salt-affected soils exist on every continent across the globe and under practically every type of climate (Dagar et al. 2019). In fact, over 6% of the world's total land area is affected by salt (Munns and Tester 2008). Salinization of soil either occurs naturally due to weathering processes of rocks, increasing sea levels, limited precipitation, and rapid surface evaporation, or is produced by human activities such as improper irrigation practices and replacing perennial vegetation by annual crops (Munns and Gilliam 2015; Parihar 2015; Quamruzzaman et al. 2022). The presence of excessive salt in the agricultural lands leads in most cases to interrupted plant growth and loss in crop production. The two major salt-induced effects on plants exposed to salinity are osmotic stress and ion toxicity: the existence of salt ions in the root medium decreases water potential and limits water and nutrients uptake by the roots. The accumulation of salt ions for a long time in soil also increases the accumulation of Na^+ and Cl^- in plant parts until it reaches toxic levels that disturb the essential biological, physiological and biochemical processes like metabolism and photosynthesis.

The ability of plants to develop and finish their life cycle under high salinity is known as salt tolerance (Parida and Das 2005). Several biochemical, physiological, structural, and molecular mechanisms underlie the plant's capacity to withstand salt stress. However, salinity tolerance differs depending on the crop types. In cereal crops, the key traits that have been suggested as indicators of salt tolerance include: exclusion of salt ions (Na^+ and Cl^-) from the leaves via limiting its absorption from the roots or compartmenting it into old leaves; discriminating between K^+ and Na^+ ; osmotic adjustment via the accumulation of inorganic ions and organic solutes like amino acids and low molecular sugars; in addition to compartmentation of Na^+ and Cl^- ions into the vacuoles; tissue tolerance through tolerating high concentrations of Na^+ in the leaves; and finally the existence of enzymatic and non enzymatic antioxidant defense system (Ashraf and Harris 2003; Munns and James 2003; Colmer et al. 2005; Colmer et al. 2006). Thus, using salt tolerant crops can be a low-cost strategy for agriculture.

Wheat is the most extensively cultivated cereal in the world as it provides a source for carbohydrates, proteins and energy for daily human nutrition. Wheat is generally grown under irrigated or rain fed conditions, thus, its culture has been always threatened by salinity. In addition, it is more susceptible to salt than other field crops, which inhibits plant growth and development and results in low productivity or even crop loss under extremely severe salinity (Sabagh et al. 2021).

On the other hand, the great efforts that have been made to breed for salt adapted varieties have been slow to catch up because of the vast knowledge gap in understanding the genetic basis of salinity tolerance and its misuse (Mujeeb-Kazi et al. 2019). In addition, domestication and breeding of the current modern varieties happened at the expense of the ability to adapt salt stress, which has led to a narrower gene

pool (Botella et al. 2005). This draws attention to conserving and exploiting the existing variation in wheat landraces to increase wheat production under salt conditions.

The Algerian Saharan oases wheat have recently gained the attention of many researchers who evaluated the genetic variation in this germplasm and pointed out the possibility of existence of a valuable adaptation potential to its abiotic stress (Zaharieva et al. 2014; Oumata et al. 2020; Bellatreche et al. 2022). Indeed, it is expected to have interesting characters related to the adaptation to salt stress because of the drastic environmental constraints of the Sahara it encountered over time. However, no studies have been published on the degree of tolerance to salt stress and the key mechanisms that confer adaptation to salinity among oasis wheat landraces.

To evaluate crops' ability to tolerate salinity, a combination of agronomical, biochemical, and physiological characteristics may provide more accurate results alongside controlled environment conditions (Kumar et al. 2017). The use of a membership function value as a screening tool for tolerance to abiotic stress, including salt, has proven to be effective (Wu et al. 2019; Yan et al. 2020; Quamruzzaman et al. 2022; Xu et al. 2023). From this perspective, the objective of this study is to evaluate the effect of prolonged salinity on some physiological, biochemical, and agronomical parameters in ten wheat landraces from the Algerian Sahara oases. Additionally, it identifies the most tolerant landraces and highlights the most important characters that confer salt tolerance to these landraces using the membership function value.

Methods

Plant material

Plant material consisted of ten locally sourced bread wheat landraces collected from different oases from the Algerian Sahara. The landraces and their names, sources and codes are presented in Table 1.

Salt treatment

The study was conducted during 2021/2022 in a glasshouse at the University of Mentouri Brothers, Constantine, Algeria (36°20'24.0"N, 6°37'12.0"E). Seeds of the used landraces were surface sterilized and germinated on filter paper, and saturated with distilled water within closed Petri dishes for 7 days. Seedlings were transferred to plastic pots of uniform size (19×27×18 cm) at a rate of eight seedlings per pot. The pots were filled with soil that is characterized by a clay-loam texture (67.4% clay, 19.7% silt, 6.97% fine sand, 5.81% coarse sand), a pH of 8.16, an electrical conductivity of 813.66 $\mu\text{S} \cdot \text{cm}^{-1}$, and a total limestone of 22.1%.

Two experiments were simultaneously conducted in the glasshouse following a complete randomized block design with four replications for each experiment. The first experiment aimed to evaluate grain yield and some

agronomical traits while the second experiment aimed to evaluate physiological and biochemical parameters. In the two experiments, control plants were irrigated with tap water (electrical conductivity of $1220 \mu\text{s}\cdot\text{cm}^{-1}$, pH of 7.21) while treatment plants were irrigated with a saline solution prepared with NaCl (150 mM). This level was achieved through a gradual increase in NaCl concentration by 50 mM per week. After reaching this concentration, treatment pots were irrigated with salt solution every other week, while on other week irrigation was done using tap water to avoid excessive accumulation of salt in the soil.

The environmental parameters were not controlled in the glasshouse, which was subjected to the actual weather condition of the region. The average temperature during the experiment (November – June) was 1–28 °C in the morning, 15–40 °C in the afternoon, and 0–12 °C at night. The pots were exposed to natural lightening with a photoperiod of 11–14 hours and a relative humidity of 30%–50%. Necessary agronomic practices were implemented by adding fertilizer (20% N, 20% P_2O_5 , 20% K_2O , 0.10% Fe, 0.10% MgO, 0.05% B, 0.02% Mn, 0.01% Cu, 0.01% Zn), removing weed, and controlling insect and fungal infections.

After 45 days of exposure to salinity, leaves of control and treatment plants from the second experiment were sampled and the following parameters were assessed in triplicate.

Compatible solutes

Proline was estimated according to Bates et al. (1973). 500 mg of fresh leaves were grounded in 10 ml of 3% sulfosalicylic acid in ice bath. The extract was filtered and 2 ml of the filtrate was added to 2 ml of acid-ninhydrin and 2 ml of glacial acetic acid. Test tubes were incubated in a water bath for 1 h. The reaction was terminated in an ice bath. 4 ml of toluene was added followed by vigorous vortexing of the tubes. The absorbance of the superior phase was read at 520 nm using spectrophotometer (JENWAY 6700 series). Proline concentration was calculated using a standard curve prepared with L-proline.

Total soluble sugars were estimated according to Duboi et al. (1956). 100 mg of fresh leaves were extracted in 3 mL of 80% ethanol for 48 h in the dark. The extract was dried under a hot air stream and the residue was homogenized in 20 ml of distilled water. 2 ml of the diluted extract was reacted with 1 ml of 5% phenol and 5 ml of sulfuric acid. The mixture was incubated at ambient temperature for 20 min. The absorbance was read at 485 nm. Total soluble sugars concentration was determined by referring to a standard curve prepared with glucose.

Photosynthetic pigments

Chlorophyll was extracted using the method of Hiscox and Israelsta (1979). 50 mg of freshly cut leaves were suspended in 5 ml of DMSO and then incubated at 65 °C in

a water bath for 1 h until the leaves segments were fully decolorized. The absorbance of the solution was read at 665 nm, 649 nm and 480 nm. Total chlorophyll and carotenoids pigments was calculated according to Wellburn (1994).

Total free amino acids

250 mg of fresh leaves were homogenized with 5 ml of phosphate buffer (50 mM, 7.8 pH) in an ice bath. The mixture was centrifuged at $12000 \times g$ for 20 min (5 °C). To 1 ml of the supernatant, we added 1 ml of 10% pyridine and 1 ml of acidic ninhydrin. The mixture was incubated at 100 °C in a water bath for 1 h, and the mixture was then to diluted 25 ml (Hamilton et al. 1943). The absorbance of the solution was measured at 625 nm. The concentration of free amino acids was determined against a calibration curve prepared with known concentration of leucine.

Hydrogen peroxide and lipid peroxidation

Hydrogen peroxide was assayed as described by Sergiev et al. (1997). 500 mg of leaf tissues were homogenized with 5 ml of 0.1% TCA using pre-chilled mortar and pestle in an ice bath. The homogenate was centrifuged for 15 min at $12000 \times g$ (5 °C). 0.5 ml of the supernatant was reacted with 0.5 ml potassium phosphate buffer (10 mM, 7 pH) and 1 ml of KI (1M). The absorbance of the mixture was read at 390 nm. The concentration of hydrogen peroxide was calculated referring to a standard curve established with known concentrations of H_2O_2 ranging from 0.2 to 0.8 nmol/ml.

Lipid peroxidation was determined by estimating malondialdehyde (MDA) content in leaves according to Health and Paker (1968). 100 mg of fresh leaves was homogenized in an ice bath with 1 ml of 0.1% TCA. The homogenate was centrifuged for 15 min at $15000 \times g$ (5 °C). 0.5 ml of the supernatant was mixed with 1.5 ml of 0.5% TBA prepared in 20% TCA. The mixture was heated in a water bath at 95 °C for 25 min. The reaction was ended by placing tubes in an ice bath. The absorbance was measured at 532 nm and 600 nm. MDA content was calculated using an extinction coefficient of 155 mM^{-1} .

Determination of ions

Leaves were washed with distilled water and then oven dried at 80 °C. 100 mg of leaf powder was digested in 10 ml of 1N hydrochloric acid overnight with mechanical shaking at room temperature. The extract was filtered into 100 ml flask and made up to 100 ml with distilled water (Asch et al. 2022). Samples were passed through flame photometer (JENWAYPFP7). Na^+ and K^+ content was determined against standard curves established with KCl and NaCl.

Electrolyte leakage

Relative membrane permeability was estimated as reported by Yang et al. (1996). 500 mg of leaf tissues were emerged in 20 of distilled water. Tubes containing samples were vortexed and kept at room temperature for 2 h (23.5 °C). The initial electrical conductivity was recorded (EC_0) using Jenway 4510 Conductivity meter. Tubes were kept at 5 °C overnight and EC_1 was recorded. After that, tubes were boiled at 100 °C and EC_2 was recorded. Relative membrane permeability was calculated as follows: $((EC_1 - EC_0) / (EC_2 - EC_0)) \times 100$.

Relative water content

Relative water content was estimated according to Barrsand Weatherley (1962). Fresh weight of fully expanded leaves was also recorded (FW). Leaves were emerged in distilled water for 24 h to record turgid weight (TW). The leaves were then oven dried until constant weight, and dry weight was recorded (DW). RWC was calculated following the equation: $((FW - DW) / (TW - DW)) \times 100$.

Estimation of agronomical traits and grain yield

The second experiment was conducted to evaluate grain yield and agronomical traits: flag leaf area was measured as suggested by Yang et al. (2016): $FLA = FLL \times FLW \times 0.75$, plant height, number of fertile tillers, number of infertile tillers, number of grains per plant, thousand grains weight and grain yield per pot were estimated for at least 10 plants.

Evaluation of salt tolerance

The salt tolerance coefficients for each trait were calculated using the following equation according to Quamruzzaman et al. (2022):

$$STC = \frac{\text{Value for salt treatment}}{\text{Value for control treatment}} \times 100$$

The calculated salt tolerance coefficients were used to estimate the membership function value (MFV) of salt tolerance for each landrace as follows (Wu et al. 2019):

$$MFVS1 = \frac{STC_i - STC_{min}}{STC_{max} - STC_{min}} \quad MFVS2 = 1 - \frac{STC_i - STC_{min}}{STC_{max} - STC_{min}}$$

where STC_i is the salt tolerance coefficient of a given landrace, and STC_{min} and STC_{max} are the minimum and maximum salt tolerance coefficients amongst all landraces. The MFVS1 was used for traits in which higher values indicate higher salt tolerance while MFVS2 was used for traits in which the increase indicates less salt tolerance. The MFVS values of 19 studied traits for each landrace were averaged to obtain values that range from 0 to 1. Landraces were ranked tolerant when $MFVS = 0.5$ or higher, moderately

tolerant when the MFVS is between 0.3 and 0.5, sensitive when MFVS is below 0.3 (Quamruzzaman et al. 2022).

Statistical analysis

The collected data were analyzed for descriptive statistics (Mean and standard deviation), graphs, and Fisher's least significant difference (LSD) at a 5% level of significance, to compare mean values of control and treatment, stepwise multiple linear regression using standardized data (salt tolerance coefficients) and Pearson correlation coefficient utilizing XLSTAT 2016 V1.0 (v18) statistical package (XLSTAT Addinsoft Inc., New York, NY, United States). General Linear Model ANOVA analysis using IBM SPSS statistics 26 (SPSS Inc., Chicago, IL, USA) was also conducted to examine the significance of the effect of landrace, salinity and their interaction.

Results

The results of ANOVA presented in Table 2 demonstrated that the effect of landrace, salinity as well as the interaction effect of Landrace $\times$ salinity were highly significant for all the studied traits.

Table 1. Name, source and code of used oasis wheat landraces.

code	Local name	species	source
L1	Bassa	<i>Triticum durum</i> Desf.	Touggourt
L2	fritass	<i>Triticum durum</i> Desf.	Touggourt
L3	Bourione	<i>Triticum durum</i> Desf.	Touggourt
L4	Magarin	<i>Triticum durum</i> Desf.	Touggourt
L5	Oum Rokba El Baida	<i>Triticum aestivum</i> L.	Touat
L6	Chater	<i>Triticum aestivum</i> L.	Touat
L7	Oum Rokba Elhamra	<i>Triticum aestivum</i> L.	Touat
L8	Khellouf	<i>Triticum aestivum</i> L.	Oued Righ
L9	Tazi	<i>Triticum aestivum</i> L.	Touat
L10	Zeghlou	<i>Triticum aestivum</i> L.	Touat

Effect of salinity on compatible solutes

Salinity resulted in highly significant changes in proline content for all landraces except for L8 which showed no significant changes when subjected to salinity (Fig. 1a). Under control conditions, L6 recorded the highest proline content (40.980 $\mu\text{g/g}$ FW) while L4 accumulated the lowest concentration (3.87 $\mu\text{g/g}$ FW). On the other hand, under stress conditions, L7 recorded the highest value of proline content compared to other landraces (98.8 $\mu\text{g/g}$ FW). All landraces significantly increased proline content as compared to control except L6 which manifested a significant decline in it. The percentage increase of proline in these landraces varied from 3% in L8 to 85% in L4.

The results presented in Fig. 1b show that landraces responded differently to salinity with regard to total soluble

Table 2. General linear model ANOVA of physiological, biochemical, and agronomical traits.

	Landrace	Salinity	Landrace × salinity	Error
Proline (µg/g FW)	1587.806***	3181.506***	955.125***	0.592
Total soluble sugars (mg/g FW)	548.005***	7.204***	57.97***	0.117
Total chlorophyll (mg/g FW)	3.722***	9.6***	2.295***	0.045
Carotenoids (mg/g FW)	0.111***	0.107***	0.112***	0.004
Total Free amino acids (mg/g FW)	17.104***	3.234**	3.708***	0.246
Hydrogen peroxide (nmol/g FW)	4.361***	19.723***	1.364***	0.181
Malondialdehyde (nmol/g FW)	138.211***	303.300***	171.684***	0.257
Na ⁺ (mg/g DW)	86.646***	248.596***	32.364***	0.041
K ⁺ (mg/g DW)	470.499***	401.244***	171.052***	0.554
K ⁺ /Na ⁺ ratio	124.928***	174.865***	9.269***	0.227
relative water content %	63.309***	694.348***	20.21***	0.455
membrane permeability%	415.576***	318.966***	30.487***	0.158
Flag leaf area cm ²	626.188**	1992.604***	205.711***	21.574
Plant height cm	0.303***	0.077***	0.021***	0.001
Herbaceous tillers	10.845***	11.948***	3.208***	0.354
Spike tillers	6.537***	3.222**	1.152**	0.428
number of grains per plant	1770.772***	7155.334***	1638.938***	412.09
thousand grains weight	415.576***	318.966***	30.487***	0.158
grain yield g.pot ⁻¹	64.24***	60.94***	15.81***	2.574

Asterisk indicates significance, *** p < 0.001, **p < 0.01, ns non-significant.

sugar content. L6, L8, L9 and L10 exhibited a significant decrease in total soluble sugars, the decrease ranged from 3.99% to 28.11%. Conversely, the other landraces recorded a high significant increase that varied from 6.08% to 18.35%, this increase was more pronounced in durum wheat landraces than in bread wheat landraces.

Effect of salinity on photosynthetic pigment

A significant increase was noted in all landraces subjected to salinity excluding L6 and L7 and L3 (Fig. 1c); this increment ranged from from 0.85% in L3 to 43.11% in L5. However, L3 and L6 did not manifest significant changes in total chlorophyll content, while L7 exhibited a significantly high reduction of 36.83% in treatment plants as compared to control.

Our results showed that salinity adversely affected carotenoids in most landraces (Fig. 1d). It caused a significant reduction that ranged from 12% in L4 to 92% in L8. L6 and L10 showed no significant difference between control and salinity treatment in carotenoids. Contrastingly, carotenoids content was significantly enhanced by 15% and 52% in L1 and L7, respectively, under saline conditions.

Effect of salinity on total free amino acids

Total free amino acids increased significantly in response to salinity in all landraces except in L3, L5 and L8 (Fig. 1e). L5 and L8 showed no significant difference as compared to control, while L3 exhibited a significant decrease of 12% in total free amino acids. The highest increment was obtained by L4 with 26% more than control, whereas L8 registered the lowest value of 4% greater than control value.

Hydrogen peroxide and malondialdehyde

Salinity induced a significant accumulation of H₂O₂ in all landraces excluding L7 and L10; in these latter, the changes in hydrogen peroxide were insignificant (Fig. 1f). Percentage increase extended from 14.86% in L6 to 40.31% in L1. In parallel, lipid peroxidation estimated as MDA content significantly increased in all landraces (Fig. 2a), although, the increase was not significant in L1, L2 and L10. The maximum increment was registered in L6 with 67.42%, while the minimum increase was observed in L3 with 15.58%.

Relative membrane permeability

Relative membrane permeability was measured as the percentage of electrolyte leakage (Fig. 2f). Salt stress significantly increased electrolyte leakage in all landraces. Electrolyte leakage under salinity conditions ranged from 14.53% in L10 to 76.44% in L3.

Ions content

Landraces showed divergence in response to salinity in terms of mineral content. Firstly, significant accumulation of Na⁺ was observed for all landraces except for L7, L8 and L10 in which, no significant changes were registered (Fig. 2b). Durum wheat landraces remarkably accumulated higher concentrations of sodium under salt stress as compared to bread wheat landraces. In bread wheat, L6 register the maximum increase in sodium ions as compared to control with 39% while L5 registered a minimum decrease of 16.24%. In durum wheat, L1 recorded the

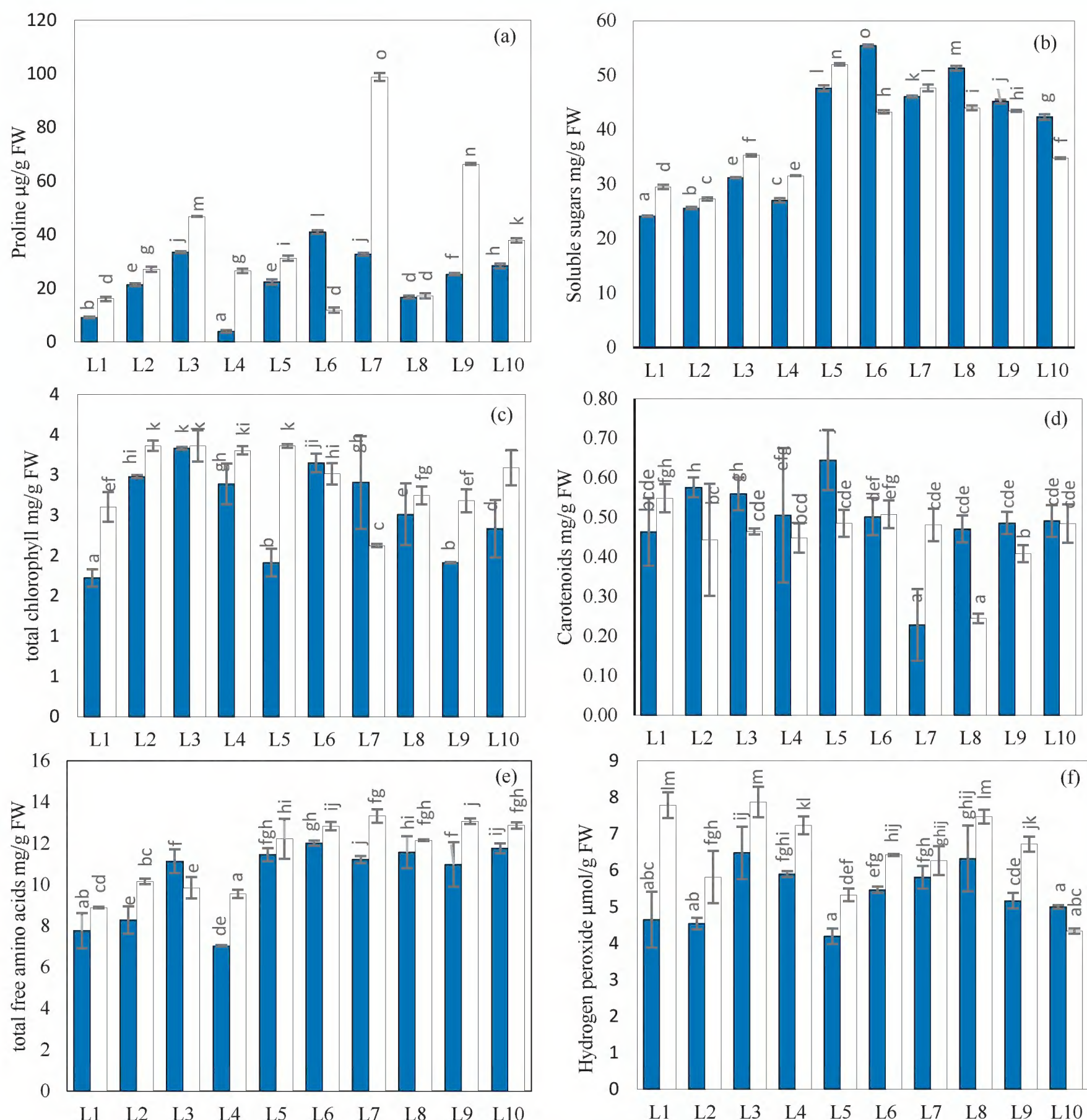


Figure 1. Effect of salinity (150 mM NaCl) on Proline, total soluble sugars, total chlorophyll, carotenoids, total free amino acids, hydrogen peroxide content of 10 landraces of oasis wheat. Data presented are mean ($n = 3$) $\pm$ standard deviation (SD). SD is presented by a vertical bar: (blue bar) control, (white bar) salinity treatment. Different lower-case indicates statistically significant difference according to Fisher's Least Significant Difference (LSD) test at 5%.

highest percentage increase in Na^+ as compared to control with 73% while L2 recorded the lowest accumulation of Na^+ with 36.80%.

Moreover, the studied landraces showed a significant decline in K^+ except in L1, L6, L8 and L9 (Fig. 2c). L8 and L9 showed no significant changes in potassium ions content under salinity. The drop in K^+ content varied from 9% to 69%. Unlike the other landraces which exhibited a decrease in K^+ , L1 and L6 unusually registered significant increment in potassium ions content when exposed to salinity stress, this increase was more remarkable in L1 (33%).

The K^+/Na^+ ratio results presented in (Fig. 2d) revealed a significant decrement in all landraces with the exclusion of L8 and L10, these latter registered no significant chang-

es. The K^+/Na^+ ratio was notably higher in bread wheat landraces than in durum wheat landraces under both control and salinity conditions. The highest decrease in bread wheat was observed in L6 with 82% decrease as compared to control. While in durum wheat, L3 exhibited a decrease that was about thrice of the control value.

Effect of salinity on relative water content

The results of RWC (Fig. 2e) showed that salinity adversely affected water content in all landraces except in L5. The maximum decrease in RWC as compared to control was obtained by L3 (15%), while minimum decrease was recorded in L7 (2%).

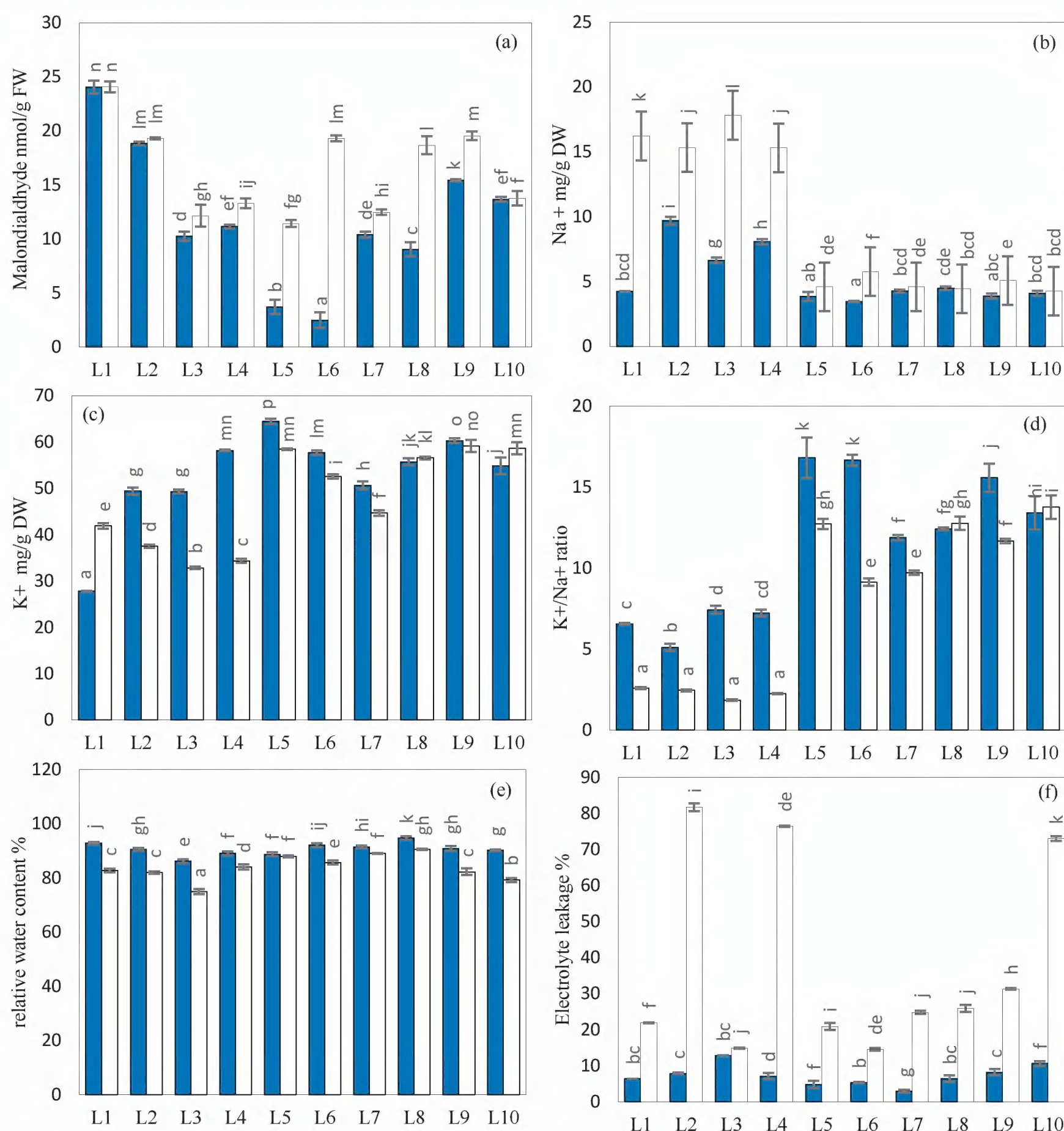


Figure 2. Effect of salinity (150 mM NaCl) on Malondialdehyde, Sodium ions, potassium ions, K+/Na+ ratio, relative water content, electrolyte leakage. Data presented are mean (n = 3) ± standard deviation (SD). SD is presented by a vertical bar: (blue bar) control, (white bar) salinity treatment. Different lowercase indicates statistically significant difference according to Fishers Least Significant Difference (LSD) test at 5%.

Effect of salinity on morphological, yield, and yield-related traits

The results of the effect of salinity on different morphological, yield, and yield-related traits are presented in Table 3. Salinity affected plant height of landraces differently. No significant changes were noticed for plant height in L1, L2, L5, L7, L8 and L10. While a significant reduction of -37%, -29%, and -10% was recorded for L3, L4 and L6 respectively. In contrast, L9 showed significant increase of 0.27%.

Furthermore, flag leaf area was negatively affected in all landraces except in L2 which exhibited an expansion in flag leaf area. However, the effect of salinity was insignificant in L1 and L10. The maximum reduction (-90%)

and minimum reduction (-14%) were registered in L6 and L7, respectively.

Moreover, salt stress didn't affect the number of vegetative tillers significantly in all landraces except in L2, L8 and L10, in which the reduction was about once and twice of the control value.

For yield related traits, the number of spike tillers significantly increased in L7 and L10 while it was not affected in the remainder landraces. The weight of thousand grains showed an enhancement of 3% in L7 while it stayed unchanged in L1. In contrast, it was reduced in the remaining landraces; this reduction ranged from -4% in L8 to 49% in L3. Furthermore, the number of grains per plant was not significantly affected in most landraces except in L3 and

Table 3. Effect of salt stress (150 mM NaCl) on agronomical traits.

Landrace	treatments	PH (cm)	FLA (cm²)	HT	ST	TGW	Gr.plant ⁻¹	GY (g.pot ⁻¹)
L1	Control	117.72 ^j	26.65 ^{bc}	1.13 ^{de}	2 ^{efg}	54.25 ^o	49.63 ^a	20.14 ^f
	Treatment	113.57 ^j	25.91 ^{abc}	1.26 ^e	2.18 ^{efg}	53.76 ^o	54.27 ^{ab}	21.71 ^f
L2	Control	120.1 ^j	21.12 ^a	2.8 ^g	2.36 ^g	45.71 ⁿ	53.72 ^{ab}	22.32 ^f
	Treatment	112.66 ^j	26.61 ^{bc}	0.8 ^{bcd}	2 ^{efg}	37.95 ^k	59.45 ^{abcd}	16.45 ^{cde}
L3	Control	78.06 ^{ef}	43.32 ^{gh}	0.6 ^{bc}	1.72 ^{def}	43.75 ^m	51.63 ^a	20.15 ^f
	Treatment	56.58 ^b	36.72 ^{ef}	0.66 ^{bc}	2 ^{efg}	29.20 ^{de}	73.18 ^{cde}	14.1 ^{abc}
L4	Control	64.96 ^c	42.21 ^{gh}	1 ^{cde}	1.63 ^{def}	34.67 ⁱ	50.09 ^a	12.17 ^a
	Treatment	50.35 ^a	30.30 ^{cd}	0.66 ^{bc}	1.45 ^{cde}	30.24 ^f	53 ^{ab}	12.46 ^a
L5	Control	86.82 ⁱ	44.75 ^{ghi}	0 ^a	0.90 ^{abc}	31.71 ^g	68.72 ^{bcde}	16.18 ^{cde}
	Treatment	84.62 ^{ghi}	36.17 ^{ef}	0 ^a	0.63 ^{ab}	32.75 ^h	59.09 ^{abc}	15.86 ^{cde}
L6	Control	77.6 ^{ef}	45.92 ^{hi}	0 ^a	0.54 ^a	38.93 ⁱ	53.18 ^{ab}	17.03 ^{de}
	Treatment	70.06 ^d	24.17 ^{ab}	0 ^a	1 ^{abc}	32.86 ^h	47.54 ^a	13.17 ^{ab}
L7	Control	83.88 ^{ghi}	49.62 ⁱ	0 ^a	0.54 ^a	37.12 ^j	45.90 ^a	20.83 ^f
	Treatment	85.8 ^{hi}	43.29 ^{gh}	0 ^a	1.18 ^{bcd}	35.07 ⁱ	68.81 ^{bcde}	21.18 ^f
L8	Control	80.7 ^{efg}	40.19 ^{gf}	0.53 ^b	1.72 ^{def}	25.29 ^c	48.18 ^a	15.08 ^{bcd}
	Treatment	76.53 ^e	25.86 ^{abc}	0 ^a	1.90 ^{efg}	24.16 ^b	76.81 ^e	15.28 ^{bcde}
L9	Control	76.96 ^e	45.31 ^{gh}	0.8 ^{bcd}	1.63 ^{def}	32.91 ^h	77.90 ^{ef}	21.15 ^f
	Treatment	81.84 ^{fgh}	33.70 ^{de}	0.46 ^b	1.90 ^{efg}	28.88 ^d	76.45 ^{ed}	17.54 ^e
L10	Control	63.66 ^c	34.60 ^{ef}	1.73 ^f	1.27 ^{cd}	29.66 ^{ef}	50.72 ^a	15.79 ^{cde}
	Treatment	63.84 ^c	34.32 ^{de}	0.6 ^{bc}	2.45 ^g	23.02 ^a	94.81 ^f	15.85 ^{cde}

PH plant height, FLA flag leaf area, HT herbaceous tillers, ST spike tillers, TGW thousand grains weight, Gr grains per plant, GY grain yield. Data are mean ±SD. Different lowercase indicate statistically significant difference according to Fishers Least Significant Difference (LSD) test at 5%.

L7, L8 and L10, in which it unexpectedly increased; the minimum increase and maximum increase were 29% and 46% for L3 and L6, respectively.

Last but not least, grain yield was not affected in L1, L4, L5, L7, L8 and L10 while it was significantly reduced in the other landraces. The maximum decline was recorded in L3 with 42.78% while minimum decline was registered in L9 with 20.56%.

Ranking of landraces

The results of MFV based on the measured physiological, biochemical, and agronomical traits are given in Table 4. The landraces were grouped into three groups according to their degree of salinity tolerance (tolerant, moderately tolerant and sensitive). Four landraces out of 10 studied landraces were identified as tolerant (L7, L8, L10). The highest value of MFV was obtained in L7 while the lowest value was noted in L3, which indicates that it is the most sensitive lan-

Table 4. Ranking of landraces based on MFVS.

Landrace	MFV	ranking
L1	0.476	moderately tolerant
L2	0.443	moderately tolerant
L3	0.252	sensitive
L4	0.479	moderately tolerant
L5	0.553	tolerant
L6	0.375	moderately tolerant
L7	0.649	tolerant
L8	0.535	tolerant
L9	0.492	moderately tolerant
L10	0.603	tolerant

drace to salinity amongst the studied landraces. The ranking of landraces from the most tolerant the least tolerant was as follows: L7 > L10 > L5 > L8 > L9 > L4 > L1 > L2 > L6 > L3.

Multiple linear stepwise regression

The results of stepwise regression analysis are presented in Table 5. For bread wheat, the results showed that only amino acids and grain yield remained in the final model by expressing significant contribution to the MFVS. The adjusted R²(=0.97) indicates that 97% of the variation in MFVS occurred due to the variation in STC of amino acids and grain yield. Hence, the prediction equation for the

Table 5. Multiple linear stepwise regression in bread and durum wheat.

independent variable	Coefficient (B)	standard error	t	P value
Bread wheat				
Intercept	-0.948	0.182	-5.213	*
Amino acids	0.006	0.001	4.480	*
Grain yield	0.008	0.001	9.995	**
R ²	0.974			
Adjusted R ²	0.956			
Cp	3.000			
Durum wheat				
Intercept	1.150	0.003	379.56	**
Grains.plant ⁻¹	-0.007	0.000	-257.69	**
Na ⁺	0.000	0.000	24.91	**
R ²	1.000			
Adjusted R ²	1.000			
Cp	3.000			

membership function value for salt tolerance (MFVS) for the accepted STCs is as follows: $MFVS = -0.947 + 6.325 \times 10^{-03} STC_{AA} + 833 \times 10^{-03} STC_{GY}$.

For durum wheat, STC of chlorophyll and number of grains per plant were the variables that contributed significantly to the MFVS while explaining 100% of the variation in MFVS (adjusted $R^2 = 1$). Thus, the prediction equation for MFVS is expressed as: $MFVS = 1.150 - 6.541 \times 10^{-03} STC_{Gr} + 1.061 \times 10^{-04} STC_{Na+}$.

Pearson correlation coefficient

Correlation analysis was conducted to examine the simple correlation coefficients between the membership function value of Salt tolerance (MFVS) and the salt tolerance coefficient (STC) for each trait (Suppl. material 1). Only K^+/Na^+ ratio, plant height, and grain yield showed significant positive correlation with MFVS. The most important positive significant correlations between physiological/biochemical traits and agronomical traits were between plant height and K^+/Na^+ ratio, number of spike tillers and Carotenoids, relative water content and thousand grain weight, and between the number of herbaceous tillers and total soluble sugars content with Na^+ content. On the contrary, the significant negative associations between physiological/biochemical characters and agronomical characters were between the number of herbaceous tillers and K^+/Na^+ ratio and relative water content.

Discussion

Plant breeders have focused on enhancing salinity tolerance in wheat over the years. Regardless, salt tolerance is still an intricate character that is influenced by genetic, biochemical, developmental, and physiological interactions. The degree of salt tolerance is also genotype-dependent, therefore, it is important to assess the response of genotypes against salinity at several levels to establish the genetic variation in salt tolerance within them.

Many researchers have conducted both on-field and pot-culture trials as part of a comprehensive analysis of salt tolerance, with each approach delivering specific strengths. Evidently, evaluating salt tolerance of genotypes in pot-culture in glasshouses provides a cost-effective method where soil heterogeneity (salinity, irrigation, and nutrients) is controlled better than on-field. In the current study, ten wheat landraces from the Algerian oasis were assessed for their salt tolerance in pot-culture at moderate high salinity (150 mM) based on a combination of agronomical, physiological and biochemical traits.

Wheat landraces are regarded as an excellent source of variation in breeding programs for tolerance to abiotic stresses (Korpetis 2023). Many researchers have pointed out that oasis wheat could be, by its origin, an interesting breeding material for abiotic stress like salinity (Benlagh-lid et al. 1990; Zaharieva et al. 2014; Oumata et al. 2020).

The results of ANOVA support the existence of wide variation within the studied landraces, as well as in their performance against salinity. In fact, the presence of diversity in germplasm proves crucial when evaluating salt tolerance, helping with the identification of the most effective genotypes. Besides, screening a genetically diverse pool increases the chances of discovering exceptionally tolerant landraces.

The membership function value has been used in many researches to evaluate stress tolerance of different crops based on agronomical, physiological and biochemical traits (Wu et al. 2019; Yan et al. 2020; Quamruzzaman et al. 2022; Xu et al. 2023). In this study, the membership function value of salt tolerance tolerance enabled grouping the studied landraces into tolerant, moderately tolerant and sensitive landraces. This result serves as an additional indication of the presence of variation in salt tolerance within the studied landraces.

Water with high concentration of dissolved salt ions leads to lower osmotic potential, which increases the osmotic stress on plant cells. To encounter osmotic stress and maintain favorable water potential, plants often accumulate organic compatible solutes like proline and soluble sugars. Our Results showed that all landraces increased proline content when exposed to salinity except L6, which experienced a drop-in proline content as well as in total soluble sugars when exposed to salinity. Similar to the findings of Poustini et al. (2007), select cultivars responded to salinity stress by lowering their proline levels. The decrease in soluble sugars was highlighted in bread wheat landraces unlike durum wheat in which soluble sugars seems to serve a crucial role in alleviating the negative effects of salinity. The most salt-tolerant durum wheat landraces accumulated the highest levels of soluble sugars. In bread wheat, the decrease in soluble sugars was marked in tolerant landraces along with the moderately-tolerant ones. However, two tolerant landraces (L5 and L7) accumulated higher soluble sugars. Aligning with these findings, Pouresmael et al. (2015) verified that one chickpea line exhibited declining soluble sugar levels when subjected to intense, sustained drought conditions over time.

Total Chlorophyll content showed an increase in both sensitive and tolerant landraces. Accordingly, Talukder et al. (2021) and Kumar et al. (2021) reported an increment in leaves' total chlorophyll of garlic and water dropwort plants treated with high salt concentration. Furthermore, Agathokleous (2020) noted that low levels of stress can enhance production of chlorophyll in some species. This enhancement can elevate the defense system of a given plant and as a result, improve their ability to adapt to environmental stress.

In the studied landraces, carotenoids increased in some tolerant and moderately-tolerant landraces. Several investigations have shown that carotenoids function as effective antioxidant compounds, conferring protection and preservation of photosynthetic light reactions during plant exposure to varied environmental stresses. Along with their important role in photosynthesis, they involve in the non-enzymatic anti-oxidant defense system by scavenging ROS (Sarvajeet 2010).

The content of amino acids was not significantly changed in some tolerant landraces (L8 and L5) while it significantly increased in the other tolerant and moderately tolerant landraces. Nevertheless, it decreased in the sensitive landrace of durum wheat (L3). Several researchers have documented an increase in the accumulation of amino acids. A recent research conducted by Hussain et al. (2021) reported a significant accumulation of amino acids in wheat cultivars subjected to salt, whereas Guellim et al. (2020) noted a reduction of amino acids in cultivars subjected to drought. Some free amino acids contribute to osmotic adjustment by playing the role of compatible solutes while others function as precursors to protein synthesis that interfere with plant response towards abiotic stress. In our study, amino acids were considered as key mechanism for salt tolerance in bread wheat as they expressed a significant contribution to the MFVS according to the stepwise regression analysis.

In the absence of stress, the production and scavenging of ROS is balanced under salinity conditions, ionic and osmotic stress result in oxidative stress, which leads in turn to an over-accumulation of ROS (Pang and Wang 2008). In most cases, the accumulation of ROS contributes to lipid peroxidation in the membrane of the plant's cell, this reaction produces many oxidation products like malondialdehyde, 4-hydroxy-2-nonenal and acrolein. In fact, MDA has been widely used by researchers as a biomarker of lipid fragmentation in many plants (Khan 2008; Masoumeh 2015). As per our observations, most landraces exhibited increased H_2O_2 and MDA content. For the tolerant landrace L10, no significant changes were recorded for MDA and H_2O_2 which might be attributed to the high detoxifying enzymatic and non-enzymatic activity of this landrace. Besides, in L7, the rise in MDA was not accompanied with significant changes in H_2O_2 ; the unchanged hydrogen peroxide content in this landrace may mask underlying enhancements in additional ROS not quantified in the present study. Indeed, the enzymatic action of lipoxygenases can also initiate lipid peroxidation resulting in oxidative degradation of lipid components within plant tissues (Farmer and Mueller 2013). Moreover, despite substantial accumulations of hydrogen peroxide in L1 and L2 under salt stress, the lack of concurrent rises in MDA implies that the oxidative degradation of lipid components may generate an array of alternative aldehyde derivatives beyond merely MDA itself that remain uncharacterized here. Notably, substantially elevated MDA levels were attained in the salt-tolerant landraces L8 and L5 upon salinity exposure. According to Morales and Munné-Bosch (2019), the increase of MDA can be an indicator of acclimation process of a plant subjected to stress instead of being an indicator of damage. It can function as a signaling molecule and activate regulatory genes related to plant defense and protection against stress. Intriguingly, the dynamics of MDA accumulation deviated substantially from expected patterns across control and treatment plants with tolerant, moderate, and sensitive lines all exhibiting sizable enhancements. Given these equivocal MDA trends disconnected from overall

tolerance capacity. Therefore, employing MDA solely as an indicative biomarker for appraising salt-induced oxidative stress may lack sufficient accuracy and reliability in these specific oasis wheat landraces.

The lipid peroxidation of the cell membrane itself can result in loss of the cell membrane integrity. Under normal condition, the permeability of the membrane is regulated by the lipid fraction along with transport proteins. When plants are exposed to salinity, the lipid fraction and membrane proteins are affected by ROS, which alters their structure. Finally, it leads to the acceleration of efflux of intracellular organic solutes and influx of sodium ions (Mansour 2013). Across conducted trials, L1 and L6 experienced moderate electrolyte leakage under stress despite the unchanged content of MDA. This can have two interpretations: either the product of lipid peroxidation is not MDA in this case, or the affected membrane integrity was much due to the oxidation of protein transport rather than the peroxidation of membrane lipids. Assessments of electrolyte leakage denoted a substantial induction uniquely evident within the salt-sensitive landrace L3. This surpassed all other investigated wheat landraces and indicated immensely disrupted semi-permeability likely stemming from irrecoverable degradation of phospholipid membrane constituents. Meanwhile, L4 (moderately tolerant) displayed the lowest membrane injury. In the tolerant landraces, maintaining membrane stability arises from enhanced endogenous non-enzymatic and enzymatic antioxidant scavenging systems.

during prolonged exposure to supra optimal sodium chloride, sodium ions present in the rhizosphere solution are readily taken up by root cortical cells through constitutively expressed channels as well as secondary active transport mechanisms, with resultant dissemination of absorbed monovalent cations via the transpiration stream to distal aerial organs. The over-accumulation of Na^+ in the tissues finally leads to ion toxicity. Moreover, the uptake of Na^+ occurs at the expense of K^+ . As a result, long-term restriction of K^+ influx disturbs the cellular metabolism.

In our study, higher concentration of Na^+ were accompanied with low K^+/Na^+ ratio in durum wheat. In contrast, lower Na^+ accumulation with high K^+/Na^+ ratio was observed in bread wheat, these results are in accordance with the findings of (Gorham et al. 1987). This divergence is due to the existence of *Kna1* locus in the 4D chromosome of bread wheat which is responsible for controlling of Na^+ accumulation and high K^+/Na^+ discrimination (Colmer et al. 2006). The absence of Na^+ accumulation in L7, L8, and L10, unlike the other landraces, indicates that they pursue mechanisms to restrict the Na^+ uptake. According to Colmer et al. (2005) and Munns and Tester (2008), tolerant landraces possess the ability to regulate Na^+ homeostasis either by Na^+ exclusion or by compartmenting Na^+ into vacuoles, leaf sheaths, old leaves and other parts of the plants, to avoid the toxic accumulation of sodium ions in tissues that are metabolically active.

Additionally, Potassium is an indispensable macronutrient for plant growth, it intervenes in protein synthesis,

enzyme activities and helps maintain the turgidity of the cell. In addition, K^+ is preferentially taken up by roots from the soil, and most plants are highly discriminating between K^+ and Na^+ (Horie 2009). Thus, the ability to keep K^+ homeostasis together with high K^+/Na^+ ratio constitutes a physiochemical selection benchmark of tremendous interest and priority for crop improvement programs. L1 and L10 had their K^+ content increased while L8 and L9 were able to keep the K^+ similar to control. Similar results were verified by Cuin (2008) where sensitive lines reduced cytosolic K^+ , contrarily to tolerant lines which raised their K^+ content. Additionally, Haq et al. (2003) reported an increment in K^+ in the salt tolerant cultivar which was attributed to the K^+/Na^+ discrimination ability of the cultivar. Correspondingly, only L8 and L10 maintained their K^+/Na^+ ratio under salinity suggesting that the uptake of Na^+ was much greater than K^+ uptake in L1 and L9.

Considering the equivalent exposure to osmotically-impacted rhizosphere salinity across assessed wheat landrace accessions, physiological analyses indicated substantive foliar dehydration uniquely manifesting within the salt-sensitive landrace L3.

Investigating morphological traits is also important in evaluating salt tolerance in crops as they determine plant growth. Plant height is a crucial trait that affects wheat's productivity and sustainability. It is used to estimate crop growth and nitrogen absorption (Jiang et al. 2020). In the current study, plant height was much reduced in the moderately tolerant and sensitive landraces. However, it was exclusively increased in L9, similarly to Qados (2011), who noted an increment in plant height under low and medium salt concentrations. Furthermore, flag leaf area also was reduced with the same pattern in tolerant landraces as well as in moderate and sensitive ones. Reduced cell elongation and cell division over days over days of exposure to salinity causes a delayed leaf appearance and a smaller final size. Leaves become smaller as a result of a shift in cell size that reduces area more than depth (Munns and Tester 2008). Nevertheless, the reduction in flag leaf area might be beneficial in terms of reducing leaf transpiration to alleviate the effects of physiological drought caused by salinity. Notably, L2 demonstrated a divergent capacity to potentiate foliar surface area upon salt exposure; a similar observation was reported by Dikobe et al. (2021). A study conducted by Guo and Schnurbusch (2015) associated increased foliar surface with detillering. In L2, the significant decrease in tillers as a result of salinity might have contributed to the larger leaf area.

Salt stress also decreased the number of herbaceous tillers in some tolerant and moderately tolerant landraces, which is in accordance with the findings of Haq et al. (2003). This decrease might diminish the competition for nutrients and resources of non-fertile tillers with fertile tillers and main stem.

An effective approach to examine linkages between salinity stress and associated biochemical/physiological perturbations involves quantitative analyses of consequent effects on reproductive yield components. Further-

more, augmenting viable grain output has constituted the foremost breeding objective across decades of genetic improvement programs focused on wheat and other cereals. This priority reflects that grain yield represents the cumulative outcome of the entirety of growth processes occurring throughout development. Assessing grain yield potential and its components under stress conditions is crucial. Over the course of this investigation, certain tolerant landraces, namely L1 and L4, which displayed moderate stress tolerance, achieved equivalent grain yields under control and stress conditions. This yield stability under variable environments suggests retained productivity despite imposed stresses for these particular landraces. According to Miransari and Smith (2019), plant growth and yield production are significantly decreased under salt stress; however, tolerant crop plants can produce higher yields under moderately high salinity. TGW was lowered significantly in all landraces except in L5, this result is supported by the findings of Akram et al. (2002). This decline in grain weight occurs because salinity shortens the grain filling period and hastens maturity, which finally leads to reduced grain weight (Maas and Grieve 1990).

Correlation analysis demonstrated that the increase in K^+/Na^+ selectivity leads to increased grain yield. The correlation between the membership function value and salt tolerance coefficients of different traits revealed a strong association with plant height, thousand grains weight, grain yield and K^+/Na^+ ration, which means that high values of these traits under salinity will lead to increased salinity. Plant height was positively correlated with K^+/Na^+ ratio and MFV, indicating that tall landraces possess higher ability to discriminate between k^+ and Na^+ and therefore they are more tolerant to salinity. In addition, correlation results showed that the decrease in HT in these landraces is accompanied with an increase in soluble sugars, which corresponds with the results reported by Dreccer et al. (2013). It also limits Na^+ uptake from the roots. Moreover, the decrease in HT will be accompanied with higher K^+/Na^+ ratio and will assure a better water status of the plant.

Stepwise regression was used to determinate the slat to tolerance coefficient of the studied traits that explains the majority of the variation in the membership function value of salt tolerance for bread wheat and durum wheat separately. The results of this analysis emphasized the role of amino acids accumulation and grain yield in determining the salt tolerance of oasis bread wheat landraces on one side, and the contribution of Na^+ content and number of grains per plant to the salt tolerance of oasis durum wheat from the other side.

Conclusion

The current study disclosed a wide agronomical, physiological and biochemical diversity in response to prolonged moderate salinity among Algerian oasis wheat. Therefore, they can be used to expand the genetic base of modern varieties and enhance their tolerance towards salt stress.

Out of the ten studied landraces, only L3 was identified as sensitive conforming to the membership function value of salt tolerance. For bread wheat, L7, L8 and L10 were identified as the most tolerant landraces. Amino acids and grain yield explained that most of the variation occurred in MFVS in bread wheat while the majority of the variation observed in MFVS in durum wheat was attributed to the number of grains per plant and Na⁺ content. Hence, employing a combination of these traits presents a viable strategy for screening oasis wheat landraces for salinity tolerance within the framework of wheat breeding

programs. Additionally, Salt tolerance in the studied oasis was highly associated with grain yield, selectivity between K⁺ and Na⁺, plant height and grain yield. We suggest exploiting these landraces as breeding material to develop salt tolerant varieties in the future.

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Supplementary material

Supplementary material 1

Pearson's correlation coefficient between STCs of different traits and MFVS (xlsx)

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